INFLUENCE OF NEST-SITE COMPETITION BETWEEN EUROPEAN STARLINGS AND WOODPECKERS

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ABSTRACT.—I studied the nesting behavior of 40 pairs of Red-bellied Woodpeckers (*Melanerpes carolinus*), 42 pairs of Northern Flickers (*Colaptes auratus*), and 23 pairs of Redheaded Woodpeckers (*M. erythrocephalus*) during three breeding seasons, 1990–1992, in east-central Ohio. European Starlings (*Sturnus vulgaris*) and Red-bellied Woodpeckers initiated nesting at the same time in early April, whereas flickers began nest excavation in late April and Red-headed Woodpeckers in early May. Red-bellied Woodpeckers incurred the brunt of starling competition for freshly excavated nest cavities and lost 39% of their cavities to starlings. Flickers and Red-headed Woodpeckers were significantly more aggressive than Red-bellied Woodpeckers when defending their nest cavities. Fourteen percent of flicker cavities and 15% of Red-headed Woodpecker cavities were usurped by starlings. Numbers of starling interactions with both Red-bellied and Red-headed woodpeckers decreased significantly (P < 0.05) over the breeding season. Woodpecker pairs unable to avoid starling competition may not have suffered reductions in fecundity since at least some of these pairs were able to renest successfully later in the season. *Received 19 July 1993, accepted 21 Sept. 1993.*

The availability of suitable nest cavities and sites for nest cavities (i.e., dead limbs and snags) limits the reproductive success of hole-nesting birds (Cline et al. 1980, Mannan et al. 1980, Stauffer and Best 1982, Nilsson 1984, Raphael and White 1984, Cody 1985, Li and Martin 1991). The European Starling (Sturnus vulgaris), an introduced secondary cavitynesting species, is known to compete with a variety of native North American primary and secondary cavity nesters for nest sites (Howell 1943, Kilham 1958, Polder 1963, Zeleny 1969, Reller 1972, Jackson 1976, Short 1979, Ingold and Ingold 1984, Weitzel 1988). However, surprisingly few studies have been conducted in order to determine whether woodpeckers or other cavity nesters actually suffer reductions in fecundity as a result of starling harassment (see van Balen et al. 1982, Nilsson 1984). Ingold (1989a) found that Red-bellied Woodpeckers (Melanerpes carolinus) suffered significant reductions in their reproductive success when competing with starlings, but Red-headed Woodpeckers (M. erythrocephalus) did not. Kerpez and Smith (1990) found that significantly fewer Gila Woodpeckers (M. uropygialis) nested in areas of starling overlap vs areas where starlings were absent; however, they were unable to detect a similar trend in Northern Flickers (Colaptes auratus). Troetschler (1976) concluded that Acorn Woodpeckers (M. formicivorus) nesting in the presence of starlings were not adversely affected since they were able

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to excavate new nest cavities or successfully delay nesting until later in the season. Thus, although starlings interact with several cavity-nesting species for nest sites, they may not reduce the reproductive success of all of them.

Red-bellied and Red-headed woodpeckers and Northern Flickers are common primary cavity-nesting species whose ranges are broadly sympatric with European Starlings in eastern North America. In Ohio, Redbellied Woodpeckers (RBW) are locally common permanent residents, while flickers are common to abundant summer residents (Peterjohn and Rice 1991). Red-headed Woodpeckers (RHW), however, are considered uncommon in the Unglaciated Plateau region of southeastern Ohio (Peterjohn and Rice 1991). European Starlings are abundant permanent residents throughout the state. Although all three woodpecker species occupy slightly different niches (Conner and Adkisson 1977, Stauffer and Best 1982), they all have been reported to lose nest cavities to starlings (Bent 1939, Reller 1972, Kilham 1983, Ingold 1989a), and occasionally to other woodpecker species (Bent 1939, Nichols and Jackson 1987, Ingold 1989b). Moreover, since RBWs in Ohio initiate nest construction in early April at the same time as starlings (Trautman 1940, Peterjohn 1989), they could be more vulnerable to starling harassment than other woodpeckers.

I quantified the nesting phenology of these four species and identified the degree of phenological overlap among them. I also attempted to determine whether a correlation exists between the aggressive nature of each woodpecker species and its ability to defend its nest cavities against starlings and other woodpeckers. I discuss whether any of these woodpecker species is suffering reductions in fecundity as a result of harassment by starlings.

STUDY AREA AND METHODS

From the last week of March through the last week of August 1990–1992, I located active woodpecker and starling nest cavities on the Muskingum College campus in the city of New Concord and on several agricultural areas near New Concord. The study area covers about 1000 ha in Muskingum and Guernsey Counties and constitutes a variety of habitats. The campus and city are characterized by a variety of hardwood species dominated by maples (*Acer* spp.), surrounded by lawns, houses, buildings, and streets. The agricultural sites consist primarily of pastures used primarily for grazing, with occasional planted fields, streams, scattered hardwoods, and snags. At several locations, patches of trees from 0.25 ha to ca 5 ha border pastures and cropland. These woody patches are dominated by black locusts (*Robinia pseudoacacia*), American sycamores (*Plantanus occidentalis*), beeches (*Fagus grandifolia*), oaks (*Quercus* spp.), and maples.

Since starlings and RBWs initiated nesting at the same time, RBW pairs were categorized as either competitors or controls (competition free). Pairs were considered controls if I did not detect starlings in a 0.25 circular ha around their nest site throughout the nesting season (cf Ingold 1989a). Although this method of categorization is somewhat arbitrary and does

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not preclude possible contact between some control woodpeckers and starlings, this criterion is fairly rigorous and makes it unlikely.

I monitored each active woodpecker and starling nest for a minimum of 30 min once a week between 07:00 and 18:00 h DST to determine the status and detect possible starling/ woodpecker and interspecific woodpecker interactions. I observed woodpecker cavities where starlings or other woodpecker species were present up to 3 h/week. Interactions were considered to occur when the individuals involved acknowledged each other's presence. Such acknowledgments included vocalizations, pursuit flights, or physical confrontations at the nest cavity (cf Ingold 1989a). I quantified all interactions, noting the aggressor and subordinate in each. Each week I climbed to those cavities that could be reached to confirm occupancy and nest status. Nest contents were examined with a light and mirror. In order to facilitate individual recognition of the woodpeckers, I captured and color-banded as many adults and nestlings as possible throughout the study.

I used Kolmogorov-Smirnov tests to determine whether differences existed in the timing of nest construction, incubation, and the presence of nestlings and fledglings in starlings, RBWs, and flickers among years (thus 12 tests were conducted on each species). Eleven of 12 tests on starlings were not significant (P > 0.05), while 10 of 12 tests on RBWs and flickers were not significant (P > 0.05). For this reason, and because my sample sizes are small (N = 17, 16, and 12 starling pairs; 9, 16, and 15 RBW pairs; and 13, 16, and 14 flicker pairs from 1990–1992 respectively), I pooled the data in all three species. The sample size of RHWs was particularly small (N = 9, 7, and 7 pairs), and I did not perform Kolmogorov-Smirnov tests. Rather, I pooled these data as well.

Since the number of interactions per/wk among starlings and woodpeckers was small and sample sizes were unequal, I tested for differences among them for the three-year period using a Kruskal-Wallis test. No differences were detected (P > 0.05) and these data were pooled. Numbers of woodpecker cavity usurpations by starlings were small, and the percentage of cavities usurped relative to the number of cavities available differed only minimally between years. These data were, therefore, pooled.

RESULTS

Nesting phenology.-Nest starts by starlings and RBWs occurred in late March and early April of all three years (Fig. 1). By the end of April, at least 75% of all active RBW nests were still being excavated, while 80% of the starling nests were in the incubation stage. Flickers initiated nest excavation about 10 days after RBWs in mid-April, and RHWs began excavating the first week of May (Fig. 1). Consequently, these species avoided the intense starling harassment that RBWs incurred in early April. Starling clutch starts, nests with nestlings, and nests with fledglings followed a bimodal pattern similar to that reported by Ingold (1989a) and Dakin (1984) in Mississippi (Figs. 2, 3, 4), suggesting that several pairs had two broods or attempted second nests after unsuccessful first nesting attempts. The incubation, nestling, and fledgling periods for RBWs, and to a lesser extent flickers, overlap with starlings, while RHWs are about two weeks behind in all phases (Figs. 2, 3, 4). The nesting period of starlings extended into mid-July (Fig. 4), and at least 38% of all pairs successfully reared two broods. Flickers fledged young through late July,

while RBWs and RHWs had active nests into August (Fig. 4). Only one woodpecker pair (RHW) was known to attempt a second brood after successfully completing a first one.

Of 40 RBW pairs observed, 12 nested in the absence of starlings. At least seven of these pairs (58%) were incubating eggs by late April, compared to only 4% of pairs competing with starlings. The proportion of competition-free RBW pairs with eggs before 15 May was significantly greater than for competing pairs with eggs before this date ($\chi^2 = 12.7$, df = 1, P < 0.001). In addition, the proportion of control RBW pairs with nestlings before this date ($\chi^2 = 9.87$, df = 1, P < 0.01). I was unable to climb to enough woodpecker cavities to determine whether or not any significant trends existed in clutch sizes, numbers of nestlings, and/or fledglings of competing versus control pairs.

Interactions.—Nesting starlings were common on all study sites except densely forested patches and were particularly abundant in town. Conversely, 96% of all woodpecker pairs nested on agricultural and forested areas outside town. Thus, although competitive interactions among starlings and woodpeckers were frequent, at least 95% of them occurred on the rural study sites.

I observed a total of 41 interactions between starlings and RBWs, all near freshly excavated RBW cavities. Twenty-nine of these (71%) occurred during April when both species were initiating nest efforts. Regression analysis reveals a significant negative correlation between the number of starling/RBW interactions and the progression of time during the nesting season (F = 10.96, df = 1,13; P < 0.01; Fig. 5). Seventeen of 25 (68%) starling/RHW interactions occurred during May when RHW were initiating nest efforts. The number of these interactions was also negatively associated with the progression of time (F = 5.46, df = 1,11; P < 0.05; Fig. 5). No definite pattern exists for starling/flicker interactions; however, most occurred during the first week of June when many flicker pairs were incubating and several starling pairs were beginning second nest efforts.

There were striking differences in the aggressive behavior of these species (Table 1). Starlings and RHWs were about equally aggressive, and both were significantly more aggressive than RBWs and flickers (contingency table Chi-square tests, P < 0.01); moreover, flickers were significantly more aggressive than RBWs (contingency table Chi-square test, P < 0.05) (Table 1).

Cavity usurpations.—Of 54 freshly excavated RBW nest cavities, 21 (39%) were usurped by starlings, thirteen during April when both species were initiating nesting (Fig. 6). Starling usurpations of RBW cavities were

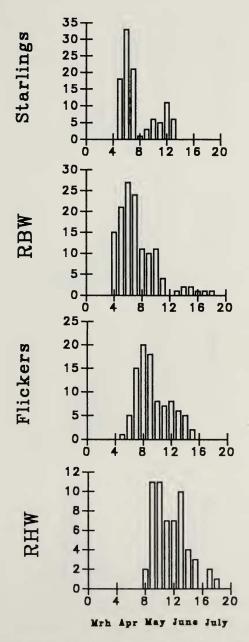


Fig. 1. Number of starling and woodpecker pairs involved in nest construction during 1990-1992 (N = 45 starling pairs, 40 RBW pairs, 42 flicker pairs and 23 RHW pairs; weeks on x axes).

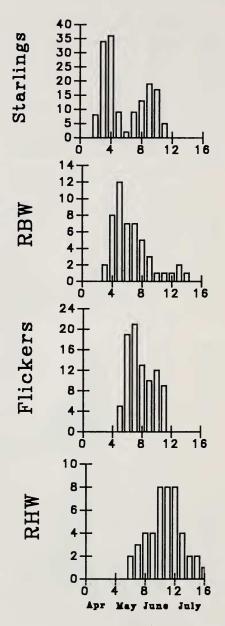


FIG. 2. Number of starling and woodpecker pairs incubating eggs during 1990-1992.

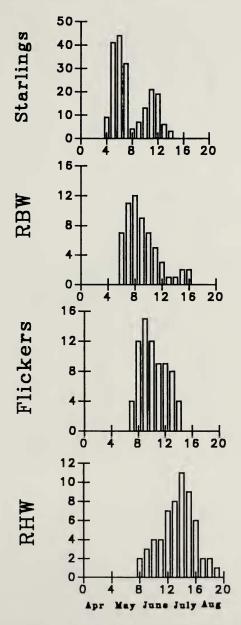


FIG. 3. Number of starling and woodpecker pairs with nestlings during 1990-1992.

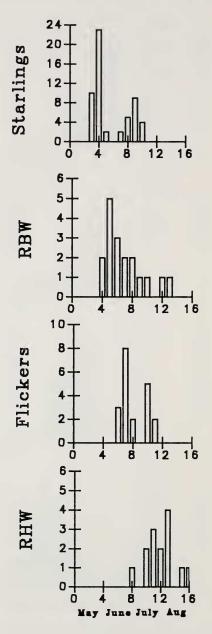


FIG. 4. Number of staring and woodpecker pairs with fledglings during 1990-1992.

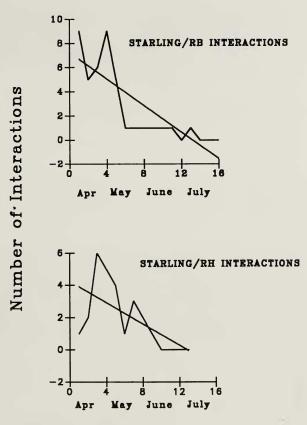


FIG. 5. The relationship between time and the number of starling/Red-bellied Woodpecker interactions per week (top; Y = 7.23 - 0.549X; $r^2 = 0.68$) and starling/Red-headed Woodpecker interactions per week (bottom; Y = 4.23 - 0.33X; $r^2 = 0.41$) during 1990– 1992.

negatively associated with the progression of time (F = 5.28, df = 1,12; P < 0.05; $r^2 = 0.37$), and only one cavity was usurped after 31 May. In addition, RBWs lost three cavities to flickers, two to southern flying squirrels (*Glaucomys volans*), and one to House Sparrows (*Passer domesticus*), relinquishing a total of 50% of their nest cavities to other species.

Seven of 51 flicker nest cavities (14%) were usurped by starlings from April through June (Fig. 6). In addition, flickers lost two cavities to RHWs and two to black rat snakes (*Elaphe obsoleta*), thus surrendering 22% of their cavities. RHWs lost four of 27 (15%) of their cavities to starlings, mostly during May (Fig. 6) and two additional cavities to House Sparrows. Because the number of starling/flicker and starling/RHW cavity usurpations was small, I did not perform regression analyses.

Aggressor species (''winner'')	Intimidated species (**loser**)				Totals
	Starling	RBW	NF	RHW	
Starling		32	16	12	60 (65%)
RBW ^a	9		5	0	14 (23%)*
NF	10	8		6	24 (41%)*
RHW	13	8	14		35 (66%)

 TABLE 1

 Summary of Competitive Interactions between Starlings and Woodpeckers at or near Nest Cavities during 1990–1992

^aRBW = Red-bellied Woodpecker; NF = Northern Flicker; RHW = Red-headed Woodpecker. Numbers in the totals column denoted with an asterisk are significantly different from undenoted numbers (P < 0.01) (contingency table chi-square tests).

Of 32 woodpecker cavities usurped by starlings, at least 22 (69%) were eventually abandoned by the starlings before egg laying. At least 11 of 18 RBW pairs (61%) that lost cavities to starlings eventually excavated a new cavity in the same $\frac{1}{2}$ circular ha or reclaimed their original cavity, but only four of these pairs (36%), to my knowledge, eventually fledged young. At least three of seven flicker pairs (43%) and three of four RHW

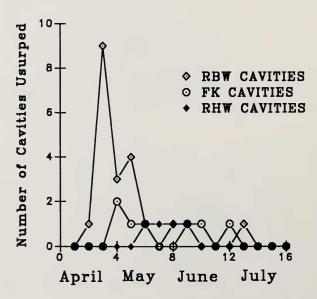


FIG. 6. Timing of cavity usurpations by European Starlings and Red-bellied Woodpeckers (RBW), Northern Flickers (NF), and Red-headed Woodpeckers (RHW) during 1990–1992 (weeks on x axis).

pairs (75%) also excavated a new nest cavity in the same ½ circular ha or reclaimed their old cavity, and of these, one flicker pair and two RHW pairs eventually fledged offspring.

DISCUSSION

These data suggest that interference competition (Levine 1976, Maurer 1984) between starlings and three woodpecker species does occur in eastcentral Ohio and is perhaps common. RBWs were particularly vulnerable to starling harassment, in part because they initiated nesting at the same time as starlings in early April; in addition, they were significantly less aggressive than starlings and other woodpeckers when defending their nest cavities. Ingold (1989a, b) documented a similar trend in Mississippi in which RBWs lost 52% of all their cavities to starlings and were significantly less aggressive than RHWs and starlings in competitive encounters.

The nesting phenology of Northern Flickers overlapped with starlings to a lesser extent, and they were also less vulnerable to starling harassment than were RBWs. By the time many flicker pairs completed cavity excavation in late April and early May, many starling pairs had already secured nest cavities and were incubating eggs. Those flickers that did encounter persistent starling harassment proved vulnerable despite their larger size. Although flickers were slightly more aggressive than RBWs, they were significantly less aggressive than starlings and RHWs when defending their nest cavities. In May 1993, I observed an attack by an adult starling on an adult flicker near a nest tree on my study site in which the starling clung to the back of the flicker while on the ground and pecked it repeatedly. Eventually, when the starling detected my presence, the flicker escaped and flew from the area. This observation, and my data in general, contrasts with those of Kerpez and Smith (1990) who found that flickers did not encounter starling competition in areas of sympatry in Arizona.

By initiating nesting in early May, RHWs were able to avoid most starling competition, since most starlings were well into their first nest effort by this time. However, not all starlings were able to find suitable nest cavities in April, and RHWs did loose 15% of their cavities to starlings, mostly in May. RHWs were as aggressive as starlings during competitive encounters at nest cavities and were often successful in driving them away. Ingold (1989a, b) found that RHWs in Mississippi lost only 7% of their nest cavities to starlings and were significantly more aggressive than starlings in head-to-head encounters.

Although nesting starlings were abundant in town and on the Muskingum campus, few woodpecker pairs (4 of 105; 4%) were found in these areas. Although excavated cavities on campus and in town appeared to be in short supply, natural knot cavities were plentiful. In fact 28 of 32 (88%) town-nesting starlings used natural cavities in six trees in which two or more starling pairs nested concomitantly within a few m of each other in knot holes. Conversely, 17 of 23 nesting starling pairs (74%) in the country used old or freshly excavated woodpecker cavities, suggesting that such cavities are more readily available and perhaps preferred over natural cavities. Although Ingold (1989b) commonly found nesting woodpeckers in town and on campus in Mississippi it is likely that the abundance of town starlings in this study discouraged many woodpeckers from undertaking nesting efforts in town.

There are advantages in maintaining differences in nesting phenologies of RBWs, flickers, and RHWs in areas where they are sympatric. However, the persistent selection pressure of starling competition could alter the timing of nesting of these species. Indeed, one consequence of interspecific competition is that it may result in a shift in the niche of one or more of the competing species (Diamond 1978, Grant 1986). Despite differences in nest-site preferences among these woodpeckers (Selander and Giller 1959; Mayr and Short 1970; Jackson 1976; Short 1982; Kilham 1977, 1983), they occasionally competed for nest sites, mostly in late April and May. RBWs are often able to avoid most nest-site competition with other woodpeckers (cf Ingold 1989a) by initiating nesting in late March and early April. On the other hand, they must compete with earlynesting starlings for nest sites. Those RBWs and other woodpeckers that are able to avoid starling competition should be at a selective advantage. However, if they delay the onset of nest initiation to avoid starlings (i.e., a niche shift), they risk increasing the period of competitive overlap with other woodpeckers which could also adversely affect their reproductive efforts.

Although my data suggest that nest-site competition is occurring, particularly among starlings and RBWs, I have only indirect evidence to suggest that one or more of the woodpecker species are suffering reductions in fecundity as a result of starling interference. Even though at least 59% of the woodpecker pairs that lost their cavities to starlings eventually returned to the same area to excavate a new cavity or reclaim an old cavity, only about 40% of these pairs eventually fledged young. Those woodpecker pairs that did not return may have also fledged young. To my knowledge, only a single woodpecker pair attempted a second brood after a successful first one. Thus, a delay in nesting caused by starlings may not be detrimental to woodpeckers if they can still fledge some young later in the season. On the other hand, such a delay may not only promote interspecific competition between woodpeckers, but it could also expose

them to food shortages and warmer temperatures that might adversely affect their reproductive success. Van Balen and Cave (1970) and Mertens (1977) found that Great Tit (*Parus major*) nestlings that hatched after the end of May were at a greater risk of incurring hyperthermia, thus reducing their chances of survival. Perhaps an even greater problem associated with such a delay might be the degree of maturity and experience that fledglings have acquired by the time winter begins. Woodpeckers produced by later nestings may be at an experience disadvantage relative to woodpeckers produced earlier in the nesting season. This could be of particular importance at more northern latitudes where winter begins much sooner than in the south. In any case, adaptive strategies resulting from starling/ woodpecker competition for nest cavities in Ohio are still emerging. Competing woodpeckers (particularly RBWs) may shift their nesting efforts to later in the season to avoid starlings, or they could nest in more densely forested areas where starlings are scarce. It is also possible that selection may favor more aggressive woodpeckers over time, because such pairs would have a higher probability of producing young that would survive to breed.

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